

The Mating System of *Vanessa kershawi*: Males Defend Landmark Territories as Mate Encounter Sites

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Abstract. Males of *Vanessa kershawi* (McCoy) occupy perch territories in the late afternoon in sunspots on hilltops and other locations in southwestern Australia. Perching males respond to intruders with chases and ascending flights, with some individuals defending the same perch site for several consecutive afternoons. Females visit territories strictly to mate and not to use any resources in these areas. In the absence of hilltops males wait at sites where local topography and vegetation create passageways that might channel dispersing females to them. Landmark-based mating systems of this sort appear to evolve in species whose females are highly dispersed because of the distribution of the food and oviposition resources that they exploit.

Introduction

Although the painted lady butterflies — genus *Vanessa* — are common and widespread, relatively little is known of their reproductive behavior. Accounts of *V. atalanta*, *V. cardui*, *V. caryae*, and *V. indica* indicate that males of these species go to certain conspicuous landmarks, particularly hilltops, but also forest-meadow edges, where they perch in the late afternoon (Alcock, 1984; Bitzer & Shaw, 1979(80); Niimura, in Suzuki, 1976; Scott, 1975, 1986; Shepard, 1966; Shields, 1967). Although males of some species are territorial, defense of the perch site does not occur in several of these species when population densities are high (Alcock, 1984). It has been assumed that perched males on hilltops and other landmarks are awaiting the arrival of receptive females, but no observations of copulations at these sites have been recorded in the literature.

This report describes the reproductive behavior of *V. kershawi* (McCoy), an abundant species throughout Australia (Common & Waterhouse, 1972). Some authors consider *V. kershawi* to be a subspecies only of *V. cardui* (Zimmerman, 1958), and there is no question that the two are very similar. We show that this butterfly uses landmarks as mate-encounter sites but that in different locations males establish territories at very different kinds of landmarks. We discuss the significance of this finding for an understanding of landmark-based mating systems, as well as documenting that landmark territoriality is associated with mate-acquisition in this species.

Methods

The butterflies were observed on 6–7 October at Tutanning Reserve, approximately 25 km east of Pingelly and 175 km southeast of Perth, W. A., on 18–19, 23–24 October and 19–20 November at Watheroo National Park, W. A., in the south-central portion of the park about 250 km north of Perth, and from 29 October to 13 January at King's Park, an area of natural bushland in Perth, W. A. The descriptive data were largely collected by selecting a site that contained a male perched on the ground in the late afternoon and then recording the behavior of the male or males that resided in that location for periods ranging from 10 min to 2.5 hr. In some cases resident males were captured in an insect net and marked with Liquid Paper typewriter correction fluid through the folds of the net before being released. The sites at which males were observed were checked again on subsequent days to determine if some perch sites were used repeatedly.

Means are presented ± 1 S.D.

Results

Perch Site Selection

In all three study sites, males arrived at their perching sites on the ground in sun spots or sunny strips in the mid- to late-afternoon. Although on some days males arrived as early as 1500 hr, the density of perching males was greatest between 1700–1800 hr in all three places. All males were gone from their perching areas by dusk. But the vegetation and topography of the areas in which males chose perch sites varied considerably among the three locations. At Tutanning, males selected sun spots on moderately forested hilltops, particularly on the edge of rocky escarpments, but also on the flat "plateaus" of the hilltops, sometimes dozens of meters from the steep hillsides. The sunspots were scattered among a forest of *Eucalyptus wandoo* and *Casaurina huegliana*.

In King's Park there are no well-defined hilltops but instead gently rolling terrain with gradual ascents and descents. At this site males were found throughout the area perched on concrete pathways (Fig. 1) and cleared firebreaks, with no obvious concentrations on the higher elevations. The paths and firebreaks cut through a forest of *Banksia*, *Casaurina* and *Eucalyptus marginata* in places and elsewhere through more open stretches of tall shrubs, mainly blackboys (*Xanthorrhoea preissii*).

In Watheroo National Park the terrain was almost completely flat and the forest an open one composed of pricklybark (*Eucalyptus tottiana*), scattered *Banksias*, and zamia palms (*Macrozamia reidleyi*). Males perched in sunny avenues in the woodland, particularly in one area where low pricklybark foliage formed a green barrier; the descending sun illuminated a long strip of ground parallel to the barrier.

Territorial Behavior

Perching males flew up at objects moving near them including stones and chunks of wood thrown over them, as well as flying dragonflies, other butterfly species, and even birds. In addition perched males sometimes spontaneously flew 2–10 m away from their perch before returning to land usually at or near the previous perching area. These spontaneous “patrol flights” occurred at the rate of 8.7/hr based on 360 min of observation of focal males in the three locations.

If at any time, a conspecific male entered the perching area, a chase invariably resulted. Whereas chases of non-conspecifics lasted only a few seconds, chases of fellow males regularly lasted about 30 sec ($\bar{X} = 28.9 \pm 17.0$ sec, $N = 36$, range 7–75). Chases began with horizontal dashes, roughly 5–15 m in length and oriented back and forth over the territory. Chases lasting more than 10–15 sec usually terminated with rapid ascending flights that took the participants 5 or more meters high, far away from the territory and out of view of the observer in woodland habitats.

The frequency of male-male interactions varied from 18.4/hr (based on 5 hr of observation) at Tutanning to 5.7/hr (11.3 hr of observation) at King’s Park, and 4.7/hr (4.25 hr of observation) at Watheroo. Generally only one male returned from a chase to perch at the site which had been occupied before the interaction. Thus males used chases to monopolize perching sites and to disperse their rivals. At King’s Park and at Watheroo perching males were separated by at least 25 m on most days. At the highest density site (Tutanning Reserve) a maximum of 11 males occupied an area of 1452 m² with a minimum distance of 6.3 m between nearest neighbors ($\bar{X} = 9.1$ m, $N = 9$). Note that it was at this site that interactions among males were most frequent.

Some males were able to control a territory for substantial periods of time in an afternoon. At King’s Park we secured 15 records of identified males (either marked with Liquid Paper or with distinctive wing damage) that held their site for a minimum of 30 min in an afternoon (up to a maximum of 140 min). Six marked males showed considerable site tenacity by returning to their perch site on the same day as capture, despite the trauma of netting. Residents generally succeeded in repelling intruders, winning 46 of 53 interactions sampled on seven days and involving five different residents at King’s Park. On four occasions both resident and intruder returned to perch in the same general area and only in three cases did the intruder replace the resident.

Some males were also able to reclaim the same location on several days. In the 10 day period from 9–18 November, all resident males (10) at one territory in King’s Park were identified by marks or wing damage, and the area checked daily. Table 1 shows that during this time three territory owners returned to the site on more than one day. In addition, a different male defended the same location for the four days

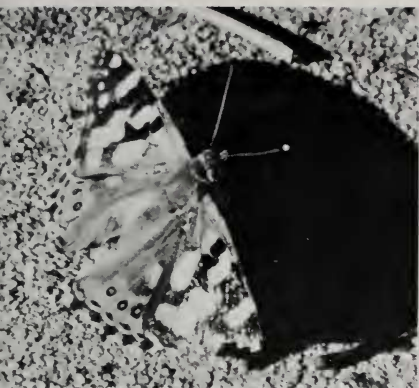


Fig. 1. A male *Vanessa kershawi* perched in a sunspot on a concrete sidewalk slab in King's Park, Perth.

Fig. 2. A frequently occupied perching area in King's Park, Perth. Males defended concrete slabs in the left hand lane of the track in the middle of the figure. Note that the surrounding vegetation creates a tunnel of sorts over the perching area.



Fig. 3. A copulating pair of *Vanessa kershawi* that mated after the female flew to the male's landmark territory on a hilltop in Tutanning Reserve, W.A.

between 26–29 November. Thus at least under some conditions males exhibit site tenacity.

But the competition for perch ownership also led to turnovers. On seven occasions when observing an identified male at King's Park or Tutanning, a new male replaced the past owner after a chase or series of chases. Thus some perches attracted more than one male owner in a single day (see Table 1), and the same spot could be occupied over a series of days by many different males. At Watheroo one site that was held on 19, 23–24 October was also claimed a month later on 19 November. A focal territory at King's Park was held by six different residents during 9–18 November and at least four other males visited the site. The recorded number of visitors is surely a gross underestimate of the actual total because most intruders were promptly chased away before they could be captured, marked or identified. The focal territory at King's Park was occupied by a resident male on 20 of 22 afternoons when the site was checked from 29 October to 13 January. Three other sites on a transect of King's park paths 420 m long were also occupied on a majority of these days (Site B = 15/22, Site C = 13/22, and Site D = 14/22).

Male-Female Interactions

Encounters between males and females were rare. At Tutanning Reserve two matings were recorded, both at times of peak male density:

Table 1. Resident and visitor males of *V. kershawi* at one perching site in King's Park, Perth from 9–18 November 1985. R = resident male — present for most of observation period; v = visitor male — present only for brief period(s) before being chased away by the resident male; R* = new male takes site from previous resident site during an afternoon.

November Male	Date									
	9	10	11	12	13	14	15	16	17 ¹	18
A	R	R	R							
B	v									
C			v		v	R				
D			v							
E			v	R	R		R			
F					R*					
G							R*			
H								R		
I								R*		
J										R

¹no observations made on this day

1729 hr on 6 October and at 1733 hr on 7 October. These took place at two different territories on the edge of a hilltop when a female flew into a territory, and was pursued by the resident away from the perch site. The pair flew much more slowly and more erratically than male-male interactors, and with no ascending component to the chase. In both cases the two butterflies landed on the foliage of a sapling wandoo eucalyptus, approximately 24 and 5 m from the point of first encounter, respectively. The male landed by the female, facing in the same direction. Copulation followed quickly with no preceding wing-fluttering by the female in one instance, although in the other the female flew off the perch several times before alighting for good. Once the female had ceased moving, the male simply probed with his abdomen twisting it to the side to couple with the female, after which he turned to face directly away from his partner (Fig. 2). In both cases copulation was still in progress 1 hr after its initiation.

One mating was recorded at King's Park at 1707 on 16 November. It followed the same pattern, although in this case the female led the male on a long pursuit as she flew away from and then returned to pass over the perch territory several times before finally landing on a casaurina cone some 3 m above the ground and about 10 m from the perch site. Copulation was still in progress 30 min after it began.

Two other probable male-female interactions were seen at King's Park. One occurred at 1648 on 11 November when a male visitor with a distinctive wing mark that had been perching near the territory holder suddenly flew up after another visitor and departed. The pair flew off in the distinctive, relatively slow horizontal flight that characterized male-female pursuits but the butterflies were lost to view in the woodland. The male did not return within a hour. The second interaction took place at 1715 on 18 November when an individual, probably a female, flew into a male's territory and led him on a brief chase before landing on the ground. The male perched immediately behind the visitor and flew up when it left. The pair went into the woodland in a slow horizontal pursuit flight and were lost in the scrub. The male did not return within a minute as was normally the case in male-male chases.

Discussion

The term "territoriality" covers a variety of behavioral phenomena, but in its most widely accepted sense it refers simply to the defense of space by an individual (Brown, 1975). In this sense males of *V. kershawi* are territorial, with individuals defending perches that may be visited in the late afternoon by receptive females. The distinctive features of male-male chases, which are very different from male-female encounters and pursuits of heterospecifics, leave little doubt that male-male interactions determine ownership of a perch site. Similar behavior has been labelled "territorial" in two reviews of insect territoriality (Baker,

1983; Fitzpatrick & Wellington, 1983; but see Scott, 1986, for arguments on the absence of territoriality in butterflies).

Some perch sites are consistently occupied by many different males over a period of several months; other similar locations never attract a territory owner. What properties make a perching area worth defending? There are no flowering plants or oviposition resources in the territories of *V. kershawi*; females visit perched males solely to acquire a mate and males defend their perching areas solely to maintain a site from which to scan for incoming females. We suggest that the mating system of *V. kershawi* is based on landmarks with local topography dictating where females are most likely to be travelling, and this in turn determines where males compete for waiting sites.

As is true for a host of butterflies and other insects, prominent hilltops may serve as orientation guides or attraction points for females (Scott, 1970; Shields 1967; Thornhill & Alcock, 1983), and when hilltops are available (as at Tutanning Reserve) males of *V. kershawi* wait at the highest points. But in some regions, hilltops are absent and then males use alternative topographic features as productive waiting sites. In King's Park, many territories are on walking tracks, sidewalks and firebreaks at points where the trailside vegetation creates a passageway likely to channel or funnel passing females toward a perched male. Similarly at Watheroo males appear to wait in open sunny areas in the woodland through which traveling females might be guided by the foliage of plants beside the clearings. Thus, whatever their environment, males of *V. kershawi* seem to take advantage of natural orientation marks, clearings through vegetation, and foliage barriers to station themselves at points most likely to be visited by dispersing females. Males of other Lepidoptera that use landmarks as mate-encounter sites may also be using topographic channels and funnels that concentrate travelling females (Callaghan, 1982(83)).

Flexibility in the use of landmarks also occurs in other butterflies (Scott, 1982(83)), including *V. atalanta* (Alcock, 1984; Bitzer & Shaw, 1979(80)), whose males station themselves on peaktops in hilly or mountainous terrain, but wait in clearings and forest-meadow edges in flat, forested areas.

The use of landmark and topographic guides appears widespread in the genus *Vanessa* (Alcock, 1984; Bitzer & Shaw, 1979(80); Shields, 1967). The behavior of *V. kershawi* and *V. atalanta*, for example, is close to identical in terms of sites selected by waiting males, the nature of male-male interactions, the duration and frequency of aerial chases, the consistency with which some territories are defended from day to day, and the restriction of territoriality and mating to the late afternoon (Bitzer & Shaw, 1979(80); Dimock, 1984(85)). Why should males of these butterflies be so prone to wait at resource-less areas rather than searching actively for females at foraging or oviposition sites? The general rule among insects is that when either food or egg-laying

resources are concentrated, thereby concentrating females spatially, males focus their search at these locations (Thornhill & Alcock, 1983). In many butterflies, including *Vanessa* species whose larvae and adults feed on a wide range of hosts (Common & Waterhouse, 1972), females are often not clumped and therefore are not easy to locate (Rutowski, 1984). Under these circumstances males may be forced to wait in portions of their environment where travelling females may occasionally appear (Rutowski, 1984). *Vanessa* butterflies are well-known for their tendency to travel long distances (Johnson, 1969; Smithers, 1969).

One would predict, however, that if females of a *Vanessa* species happened to become aggregated at a restricted food- or hostplant, their males would respond by searching for mates at these productive locations. When females of *V. cardui* occur in large numbers on flowering *Encelia farinosa* in central Arizona, some males do search for mates at the foodplant (Alcock, 1984). A combination of hilltopping and searching at flowers has been reported for a few other butterflies as well as by Scott (1982(83), 1986). Likewise, 10–20 males and females of *V. kershawi* were found at a local patch of a flowering *Verticordia* on 19–20 November at Watheroo National Park. The plant had not been in bloom a month earlier when late afternoon perch defenders were common in other areas, but by 19–20 November only a single perch defender was located. Instead, throughout these days males frequently engaged in what appeared to be brief (< 5 sec) horizontal sexual chases at the foraging site. Apparently when females of *Vanessa* are spatially clustered at flowers, males travel to these locations to search for receptive partners. But if no such clusters exist, males wait at travel points for diffusely distributed females to come to them.

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